SPECIES COMPOSITION AND RELATIVE ABUNDANCE OF ADULT FISH IN PYRAMID LAKE, NEVADA

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Abstract.— Pyramid Lake fish populations were sampled with nets on a monthly basis from November 1975 through December 1977. Fish species were taken in the following order of numerical relative abundance: tui chub (*Gila bicolor*), Tahoe sucker (*Catostomus tahoensis*), Lahontan cutthroat trout (*Salmo clarki henshawi*) including cutthroat-rainbow hybrids, cui-ui (*Chasmistes cujus*), and Sacramento perch (*Archoplites interruptus*). Relative abundance estimates are discussed with respect to seasonal availability, spatial distribution of the fish, sampling bias of the fishing methods, and biomass of the fish. Recent temporal trends in the population structure of the lake are presented.

In fisheries biology a basic measure of abundance is catch-per-unit-effort, or stock density (Cushing 1968). Catch/effort (C/f) is nearly always the best available measure of the true stock density, although rarely exactly proportional (Gulland 1969). Marr (1951) termed relative abundance as determined by C/f measurements as "relative apparent abundance." Passive fishing gear such as trap and gill nets are standardly used to sample fish populations as a practical necessity because more direct methods (e.g., seining, poisoning, and mark-recovery techniques) frequently are not applicable to large natural lakes (Moyle 1950). Extensive use of gill nets over the entire growing season generally provides the best estimate of species composition, size composition, and relative abundance of lake fish populations (Powell et al. 1971, Walberg 1969).

Fish of different sizes may be caught with varying efficiency, either as a result of selectivity of fishing gear or because of differences in distribution or habitat; thus, as fish grow their vulnerability to capture changes (Ricker 1958). Therefore, it may be advisable to use two or more types of gear in estimating fish population statistics. After evaluating C/f data, Walberg (1969) concluded that trap and gill nets were most efficient for sampling adult fish. Similarly, Yeh (1977) found small hoop nets used in conjunction with gill nets to be the most efficient paired gear to estimate species composition and relative abundance.

The purpose of this research was to estimate the relative abundance of fish populations in Pyramid Lake, taking into account the reliability of the estimate with respect to inherent sampling biases. A valid relative abundance estimate of fish populations is contingent upon the representative sample on which the estimate is based; i.e., it must equal the proportion of the species in the lake. All fish sampling methods have inherent biases, however, due to interactions with fish size, distribution, habitat preference, behavior, or physical characteristics, which in turn are a function of species, age, and environmental conditions.

To obtain a valid estimate of species composition and relative abundance in Pyramid Lake, several sampling methods were used in various habitat types. Three comparative perspectives are presented (i.e., catch statistics derived from):

1. Bottom-set gill net samples stratified by depth and area during a two-year period; these data are also related to comparable historical data.
2. Four independent passive and active fishing methods, i.e., gill nets, fyke nets, beach seines and otter trawls.
3. Six distinct habitat types utilizing three different but comparable gill net fishing methods; data are weighted according

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to the proportion of the total lake volume that each habitat represents. These data are also transformed into biomass estimates.

Study Area

Pyramid Lake is the terminal water body of the endorheic Truckee River system that originates some 192 river km upstream at Lake Tahoe. Pyramid Lake is about 40 km long, with a north-south axis; its width varies from 16 km at the north to 6.5 km at the south. During 1976, the mean elevation was 1,157.3 m above sea level, corresponding to a surface area of 446.4 km^2, volume of 26.4 km^3, mean depth of 59 m, and maximum depth of 103 m (United States Geological Survey 1977, Harris 1970).

The only outflow from Pyramid Lake is by evaporation. Due to water diversions from the Truckee River, the water level of Pyramid Lake has declined 22 m since 1909. The lake water is highly ionic, being saline and alkaline with a pH of 9.2. The 1976 total dissolved solids concentration was 5,235 mg/l.

During 1976 and 1977 mean surface temperature ranged from 6.1 to 23.1 C. As winds subside and surface water temperature increases, a thermocline is formed from June through December. The lake is monomictic, turnover begins in early winter, and mixing extends to spring.

Procedures

Three east-west sampling transects were selected in Pyramid Lake that are representative of the north, middle, and south sections (Fig. 1). Four gill net stations were established along each transect, i.e., onshore and offshore on the east and west sides of the lake. I activated this sampling design in November 1975 and conducted it through December 1977. A fifth sampling station, representing a specialized habitat, was established beginning February 1976 in each section, i.e., north: Pinnacles thermal springs; middle: profundal; and south: Truckee River delta. Gill nets were set during the first week of each month at each of the 15 sampling stations. Variable-mesh, bottom-set gill nets were utilized. The 1.83 × 76.20 m gill nets were composed of ten 1.83 × 7.62 m panels of the following mesh sizes (cm bar measure): 1.27, 1.91, 2.54, 3.18, 3.81, 4.45, 5.08, 6.35, 7.62, and 8.89. The nets were built of white multifilament nylon of the following thread diameters (for respective mesh sizes): 0.23 mm (1.27 cm), 0.28 mm (1.91 and 2.54 cm), 0.33 mm (3.18, 3.81, 4.45, 5.08 and 6.35 cm), and 0.40 mm (7.62 and 8.89 cm). A total of 373 gill nets sets were made during the standardized monthly sampling program.

Supplemental sampling was conducted at various depths with the standard bottom-set gill nets. During September and December 1976 and March and June 1977, 52 bottom gill net sets were made in the profundal zone of Pyramid Lake at depths exceeding 61 m (Vigg 1980). The net sets were stratified on an areal basis within the benthic profundal zone. This sampling program further defined relative abundance of fish species with respect to bottom depths and associated environmental parameters.

In addition, five other gear types were used: surface gill nets, vertical gill nets, fyke nets, beach seines, and otter trawls. These ancillary fishing methods were utilized to obtain samples representative of all major habitat types and to facilitate evaluation of gear bias.

Vertical distribution was evaluated inshore with paired surface-bottom gill nets, and offshore with vertical gill nets (Vigg 1978). Variable mesh, surface-set gill nets were utilized to sample inshore relative fish abundance above the thermocline in conjunction with standard bottom-set gill nets below the thermocline at 23 m. The 76.20 m long surface gill nets were identical to the standard, bottom-set nets except they were 3.66 instead of 1.83 m deep and rigged to float on the surface instead of sinking to the bottom. Surface gill nets were test fished from February through May 1977 (12 samples) in conjunction with the primary monthly netting program. An intensive monthly surface-bottom netting program was implemented from June through November 1977. During this period, 35 surface samples above the thermocline and 35 bottom samples below the thermocline, at a depth of 23 m, were taken. These surface-bottom samples at 23 m were stratified by lake area along the same transects used in the primary gill netting program.

Vertical gill nets similar to those described by Horak and Tanner (1964) were utilized to study limnetic relative fish abundance. The nets, 2.44 × 45.72 m, were set overnight in gangs of eight nets of the following mesh sizes (cm bar measure): 1.27, 1.91, 2.54, 3.81, 5.08, 6.35, 6.62 and 8.89. Spreader bars physically separated each net into six 7.62 m

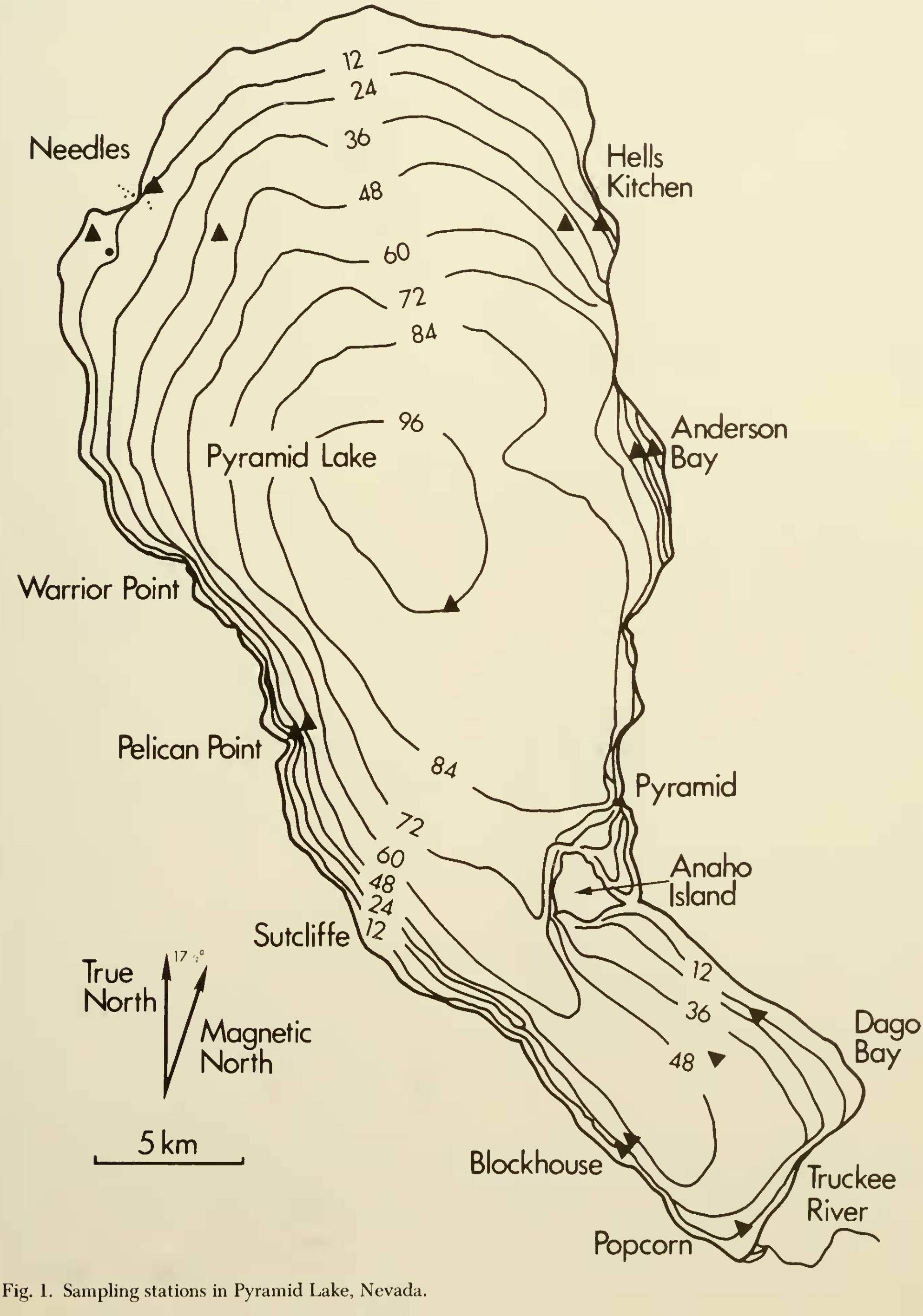


Fig. 1. Sampling stations in Pyramid Lake, Nevada.

depth increments. From December 1975 through February 1976 four large mesh vertical gill nets were test fished in offshore areas; however, bad weather made the netting inefficient and the catch rate was very low, apparently due to the large mesh sizes utilized. I implemented an intensive vertical gill netting program from June through October 1977. A total of 18 sets of gangs of eight vertical gill nets were made at a midlake limnetic station during the period on a monthly basis.

Fyke nets were set at six stratified onshore stations in conjunction with the monthly gill net samples. They were constructed of 1.27 cm bar mesh nylon netting covering four 1.22 m diameter fiberglass hoops. The extended net was 4.88 m in length with a 15.24 m lead that was set perpendicular to shore. A total of 147 fyke net sets were made on a monthly basis.

A 121.92 m beach seine (77 samples) and a 4.87 m bottom otter trawl (63 samples) were utilized in stratified lake areas from November 1975 to November 1976 on a seasonal basis. The 121.92 m beach seine with a 3.05 m deep bag of 1.27 cm bar mesh was fished in shallow areas of suitable substrate on the west shore of the lake. The seine was operated by setting it parallel approximately 30 m from shore with a small boat, then simultaneously pulling both ends of the net to shore. The 7.62 m semiballoon otter trawl with a 0.64 cm bar mesh interliner was fished on the bottom, throughout the lake, at depths up to 46 m.

Species composition was determined from the fish caught in all types of sampling gear. Relative abundance was estimated from catch statistics derived from each sampling method separately and all sampling gears combined. Relative abundance was also analyzed with respect to discrete habitat types and the proportion of the lake represented by each habitat.

Result and Discussion

The historical fish species composition of Pyramid Lake, original and introduced, is listed in Table 1. Ten species were captured during 1975–1977; the five most abundant species composed over 99.9 percent of the total catch. Tui chub was clearly the predominant species, followed in numerical relative abundance by Tahoe sucker, Lahontan cutthroat trout, cui-ui, and Sacramento perch. During this study we captured over 73,000 fish with nearly 800 net samples, utilizing six different fishing methods in a variety of habitat types (Table 2).

This catch tabulation may be considered a relative abundance estimate in itself; however, consideration of three factors is necessary for the valid interpretation of these data. Sampling bias, temporal, and spatial factors are interactive and must be weighted with respect to the ecology of the fish populations in Pyramid Lake.

Any single fishing method can introduce bias by providing a sample that is not representative of the true population. Comparison of two or more sampling methods enables at least a partial dealing with this problem. Juveniles are generally not captured in proportion to their actual abundance because their vulnerability to capture increases as they grow and the actual population size undergoes drastic changes during the first year of life. This problem is largely eliminated by ignoring the dynamic juvenile population and obtaining an index of only the adult population. Each population has a species-specific temporal activity pattern within the year. To obtain a representative sample of all species present in a lake, the sampling period must include the active season of each species. Therefore, the minimum time frame is the growing season for the fish; however, monthly sampling throughout the year is desirable to insure inclusion of the entire annual activity cycle for each species. In Pyramid Lake, the fish populations exhibit marked changes in vertical and benthic spatial distribution (Vigg 1978, 1980). For the cutthroat trout and tui chub populations, these distribution patterns interact with temporal activity cycles. Thus, various vertical and horizontal strata must be sampled to obtain a realistic sample of relative fish abundance. Pyramid Lake is a large, deep body of water with heterogeneous and discrete habitat types. The limnetic zone especially requires adequate representation in fish sampling because the offshore water column comprises over half the total volume of Pyramid Lake. Furthermore, a morphologically distinct planktiverous population of tui chubs exists in the limnetic zone of Pyramid Lake, in contrast to the benthic inshore form.

Although conventional fishing methods utilized in this research do not guarantee a sample that is exactly proportional to the true population in Pyramid Lake, consideration of the previously mentioned factors enables quantitative estimates of relative abundance. I derived three comparative estimates of relative abundance from the fish catch data (Table 3). Although it is impossible to determine which one, if any, represents the true proportion of fish populations

TABLE 1. Original and introduced fish fauna of Pyramid Lake, Nevada (after La Rivers 1962 and U.S. Department of the Interior 1975).[1]

Fish species	
Common name	Scientific name
ORIGINAL SPECIES	
°Lahontan cutthroat trout	*Salmo clarki henshawi*[2]
Pyramid rainbow trout	*Salmo gairdneri smaragdus*[3]
°Cui-ui	*Chasmistes cujus*[4]
°Tahoe sucker	*Catostomus tahoensis*
Mountain sucker	*Catostomus platyrhynchys*[5]
°Lahontan redside	*Richardsonius egregius*[6]
°Lahontan tui chub	*Gila bicolor (obesa and pectinifer)*[6]
°Lahontan speckled dace	*Rhinichthys osculus robustus*[6]
INTRODUCED SPECIES	
Kokanee	*Oncorhynchus nerka kennerlyi*
Coho salmon	*Oncorhynchus kisutch*
Rainbow trout	*Salmo gairdneri*[8]
Brown trout	*Salmo trutta*
Yellowstone cutthroat trout	*Salmo clarki lewisi*
°Cutthroat trout hybrids	
Cuttbow: male cutthroat × female rainbow	
Bowcutt: Male rainbow × female cutthroat	
Kamcutt: Male Kamloops rainbow × female cutthroat	
Brook trout	*Salvelinus fontinalis*
°Carp	*Cyprinus carpio*
Channel catfish	*Ictalurus punctatus*
Bluegill	*Lepomis macrochirus*
°Sacramento perch	*Archoplites interruptus*
INTRODUCED RESIDENT SPECIES IN THE LOWER TRUCKEE RIVER WITH ACCESS TO PYRAMID LAKE	
°Mosquitofish	*Gambusia affinis*
Black bullhead	*Ictalurus melas*
Brown bullhead	*Ictalurus nebulosus*
°Largemouth bass	*Micropterus salmoides*
Green sunfish	*Lepomis cyanellus*
Black crappie	*Pomoxis nigromaculatus*
NATIVE TO THE UPPER TRUCKEE RIVER, PROBABLY WITHOUT ACCESS TO PYRAMID LAKE	
Mountain whitefish	*Prosopium williamsoni*
Paiute sculpin	*Cottus beldingi*

°Captured in Pyramid Lake during 1976–1977.

[1]Nomenclature after Bailey et al. (1970) except for subspecies.

[2]The original strain of Pyramid Lake Lahontan cutthroat trout is believed to have become extinct in the 1940s. Nevertheless, strains of Lahontan cutthroat trout (Heenan Lake, Walker Lake, and Summit Lake) that are remnants of the original Pyramid Lake strain have been reintroduced into Pyramid Lake. Hickman and Behnke (1979) may have recently discovered a population exhibiting the genetic composition of the original strain.

[3]Not a good taxonomic unit, possibly an early introduction of rainbow trout or an atypical Lahontan cutthroat trout (La Rivers 1962).

[4]Officially considered an endangered species; occurs only in Pyramid Lake.

[5]Previously *Pantosteus lahontan*, *Pantosteus* was reduced to a subgenus of *Catostomus* (Bailey et al. 1970).

[6]Two forms of Lahontan tui chub are known to exist, i.e., *Gila bicolor obesa* (Girard), which is characterized by coarse gill rakers, and *Gila bicolor pectinifer* (Snyder), which exhibits fine gill rakers. Disagreement exists among authorities whether or not these forms represent discrete taxons. Miller (1951) and Hopkirk and Behnke (1966) consider the two forms to be distinct species. Hubbs, Miller, and Hubbs (1974) consider the two types to be subspecies that exhibit intraspecific intergradation, and La Rivers and Trelease (1952) state that *G.b. pectinifer* is not a valid taxon. Kimsey (1954) considers the tui chub population occurring in Eagle Lake best described by the scientific name *bicolor: obesa × pectinifer*. A further taxonomic complication exists because *Gila bicolor* are known to hybridize with *Richardsonius egregius* and *Rhinichthys osculus* in Lake Tahoe (Evans 1969).

[7]Pen culture of coho occurred before and during this study.

[8]Including steelhead and kamloops strains.

[9]Questionable species that may fit into this category include: Yellow perch, White crappie, White catfish, and Sacramento blackfish.

of Pyramid Lake, in the following sections I will discuss the relative merits of the estimates derived from:

1. Bottom-set gill nets
2. Four independent sampling methods
3. Six habitat types

Bottom-Set Gill Nets

It is generally recognized that variable-mesh gill nets provide the best single estimate of population statistics for lacustrine fish. Although one must realize the limitations of any single sampling method, the long-term and widespread use of bottom-set gill nets makes resultant data very useful for comparison with historical data in Pyramid Lake as well as for any between-lake comparisons.

The net used in this study encompassed a range of mesh sizes (1.27–8.89 cm bar mesh) to facilitate the capture of all species present. The selectivity curve indicates a representative sample of the adult size groups was

TABLE 2. Total species fish catch utilizing six different fishing methods in Pyramid Lake, Nevada.

Fishing gear	Habitat sampled	Time period	Number of samples	Cutthroat trout	Cui-ui
Bottom-set gill net	Inshore 0–15 m	11–75 to 12–75	153	636	289
	Offshore 46 m	11–75 to 12–77	152	496	11
	Pinnacles 0–15 m	2–76 to 12–77	23	86	40
	Delta 0–15 m	2–76 to 12–77	23	104	71
	Deep Benthic >46 m	12–75 to 11–77	72	42	0
	Inshore (Below Thermocline) 23 m	6–77 to 11–77	35	270	10
Surface-set gill net	Inshore (Surface) 23 m	6–77 to 11–77	35	47	0
Vertical gill net	Limnetic (Vertical Water Column) 0–46 m	6–77 to 10–77	18	35	0
Fyke net	Inshore 0–15 m	12–75 to 12–77	147	46	2
Beach seine	Inshore 0–3 m	12n75 to 11–76	77	149	0
Otter trawl	Inshore 0–46 m	11–75 to 8–76	63	0	4
Total	ALL	11–75 to 12–77	798	1,911	427
Percent				2.61	0.58

*Mosquito fish were captured in small pools around the perimeter of the lake with a dip net.

achieved because the entirety of the curve for each species is contained within the 10 mesh sizes of the net (Fig. 2). The ascending right limb of each species-specific curve represents recruitment to the gear and indicates that juveniles were not adequately sampled by the gill net. The descending left limb is related to mortality, i.e., numbers decrease with increasing age and size. A 2.44 × 60.96 m gill net composed of four mesh sizes (10.16–17.78 cm bar measure) progressively larger than those of the standard net was used to test how effective the standard net was in catching large cui-ui and trout. No large fish were captured with this net after 13 samples (only two small trout were caught by their teeth); this indicates that fish too large to be captured with the standard net were not abundant.

Percent species composition estimated from gill net catches compared to the other methods favored trout, cui-ui, and Tahoe sucker, and was least for tui chub. I believe the gill net samples underestimated the num-

Table 2 continued.

Fish species°							
Tahoe sucker	Tui chub	Sacramento perch	Lahontan redside	Largemouth bass	Carp	Speckled dace	Total
2,960	14,996	72	0	0	1	0	18,954
675	6,671	0	0	0	0	0	7,853
775	1,834	19	0	0	0	0	2,754
695	1,618	17	0	0	4	0	2,509
18	1,567	0	0	0	0	0	1,627
631	1,975	3	0	0	0	0	2,889
2	2,657	1	0	0	0	0	2,707
0	5,227	0	0	0	0	0	5,262
373	23,608	61	0	0	1	0	24,091
29	3,514	1	26	0	1	1	3,721
82	711	8	0	1	1	2	809
6,240	64,378	182	26	1	8	3	73,176
8.53	87.98	0.25	0.04	TRACE	0.01	TRACE	100

ber of tui chubs due to the saturation effect observed when fish densities are high. Catch rates are depressed even by moderate catches, and it is possible to saturate nets to the point that they will catch no additional fish (Kennedy 1951). Spatial elimination of net area, visual stimulus, vibrations, and alarm substances (which chubs and suckers secrete) are some factors that cause saturation of gill nets (Meth 1970). Over 400 tui chubs have been captured in one 1.83 × 7.62 m mesh panel in Pyramid Lake during a one-day set. Cutthroat trout in Pyramid Lake are probably overestimated by gill net catches because they are frequently entangled by their jaws and teeth. As a result, trout (especially large ones) are vulnerable to almost all mesh sizes and are thus susceptible to much more netting area. This is indicated by the platykurtic catch curve for trout by mesh size.

Four Independent Sampling Methods

It is important to take into account the possible underestimation of tui chub in gill net data, especially when comparing the relative standing crops of cutthroat trout and tui chubs with respect to their predator-prey relationship. As independent comparisons, fyke net catches are composed of about 99 percent tui chubs, seine catches are composed of about 95 percent tui chubs, and trawls captured no trout.

The relative proportion of Tahoe sucker to trout is about the same, based on gill and trap net data. In contrast to the other fishing methods, the seine captured five times as many trout as Tahoe sucker. No adult trout were captured in otter trawls and no cui-ui were captured in seines. The seine and trawl captured incidental species not taken by other methods.

To deal with the problem of fishing gear selectivity, the catch statistics of gill nets, fyke nets, seines, and otter trawls were used as independent estimates. By sampling during all seasons for a minimum of one year with each fishing gear, the species-specific variation in temporal availability is averaged out. Nevertheless, different amounts of fishing effort (net sets) were allocated to the various methods. Because I am assuming (for the sake of this relative abundance estimate) that each fishing method has equal validity, it is necessary to standardize fishing effort. I gave equal weight to each of the independent estimates by taking the mean of the C/f of the four sampling methods for each species, from which I calculated the percent species composition estimate. As can be seen in Table 3, inclusion of the three additional sampling methods shifts the relative abundance estimate in favor of the tui chub while not affecting the species rank. The proportions among the four less abundant species remain relatively constant.

Although the use of fyke nets, trawls, and seines compensated for the high density saturation of tui chubs in gill nets, other sampling problems existed. The various fishing methods were restricted with respect to lake zone sampled, therefore introducing spatial bias. For example, seines and fyke nets sampled only shallow water, and sienes and otter trawls could only sample areas of relatively smooth substrate.

TABLE 3. Comparison of three relative abundance estimates of the five major fish species in Pyramid Lake, Nevada, 1976–1977.

Species	Percent species composition (bottom-set gill nets) (n = 373)	Percent of mean C/f of four sampling methods (gill and fyke nets, trawl, and seine) (n = 660)	Six habitat types weighted by proportion of lake volume (bottom, surface, and vertical gill nets) (n = 174)
Tui chub	77.92	91.43	97.27
Tahoe sucker	16.00	5.82	1.38
Cutthroat trout	4.07	1.86	1.29
Cui-ui	1.28	0.38	0.03
Sacramento perch	0.33	0.22	0.01

Six Habitat Types

The gill net sampling method was more flexible than other methods and with it I was able to sample various bottom depths and habitats within the two-year monthly sampling program. Percent species composition and catch rates in the various habitats varied substantially and verified the need for a spatially stratified design for the estimation of relative abundance. These gill net samples, however, were restricted to the benthic lake areas and did not adequately represent surface and limnetic waters. We overcame these problems by sampling a total of six ecotypes with three different types of gill nets.

Additional gill net sampling was conducted in surface inshore waters and the vertical limnetic water column. Thus, I obtained a stratified areal sample (utilizing various types of comparable variable mesh gill nets) that was representative of the most important habitats of Pyramid Lake (Table 4). The species composition and C/f in six ecotypes varied remarkably. Cui-ui, Tahoe sucker, and Sacramentó perch were taken primarily in shallow inshore areas. Previously discussed relative abundance estimates gave a disproportionate weight to these shallow littoral areas due to the sampling techniques employed. Realistically, however, shallow areas compose only a small proportion of the total lake area and volume. The relative proportions of the different ecotypes are presented in Figure 3. This diagramatic separation of lake strata is admittedly arbitrary; however, considering the ecology of the fish species in Pyramid Lake and the areal differences in species diversity and relative species composition, I believe these strata represent discrete habitat types.

I calculated the third relative abundance estimate by weighting the C/f data of the six ecotypes with the proportion of the total volume of the lake each represents. Using this holistic perspective, the tui chub population composes over 97 percent of the total number of fish in Pyramid Lake. I believe this is the most realistic estimate of the relative abundance of each of the five major fish species in the Pyramid Lake fish population. Actually, tui chubs may be even more numerous

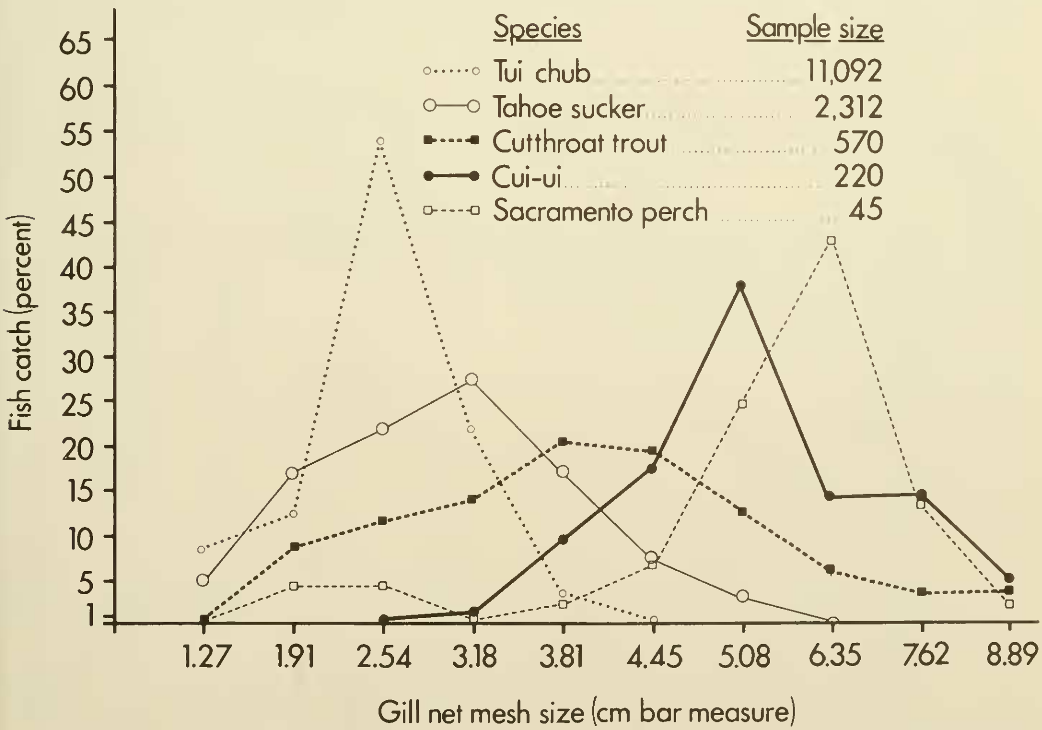


Fig. 2. Percent of the total species fish catch taken in 10 mesh sizes of variable mesh bottom-set gill nets in Pyramid Lake, Nevada, January–December 1976.

than this index indicates because gill nets in all ecotypes probably underestimate tui chubs and overestimate cutthroat trout.

Relative Biomass

The relative biomass of lacustrine fish populations is important for the evaluaton of the bioenergetics of the ecosystem. Relative biomass is a function of the species specific weight and age composition as well as the numerical abundance of the population. Mean weight of a sample multiplied by the total catch of that species yields an estimate of the total relative weight of the catch, by species. Likewise, the product of the mean weight and the relative abundance estimate provides an index of the relative biomass of the population, assuming a representative sample (Table 5).

The relative species weight composition of the approximately 73,000 fish captured by all methods (Table 2) is naturally shifted toward the larger fish such as cutthroat trout (≃10.7 percent) and cui-ui (≃7.5 percent). Although the tui chub comprises the majority of the weight of the total catch (≃67 percent), this represents a much smaller proportion of the catch than by numbers of individuals (≃88 percent). Nevertheless, as previously discussed, the total catch is not necessarily representative of the actual population, due to sampling bias. The index of relative numerical abundance presented in Table 4 is probably the most accurate basis for determining a relative biomass estimate. Thus, it is estimated that tui chubs compose about 90.4 percent of the biomass of the total fish population in Pyramid Lake and cutthroat trout compose about 6.4 percent. Theoretically, the biomass of a primary piscivor such as cutthroat trout may be as much as 20 percent of the biomass of fish forage (McConnell et al. 1978). Because cutthroat trout represent less than 7 percent of the combined biomass of tui chub and Tahoe sucker, there is apparently a substantial potential for increase in population size. In all cases the rank of species abundance remains constant.

Temporal Changes in Relative Abundance

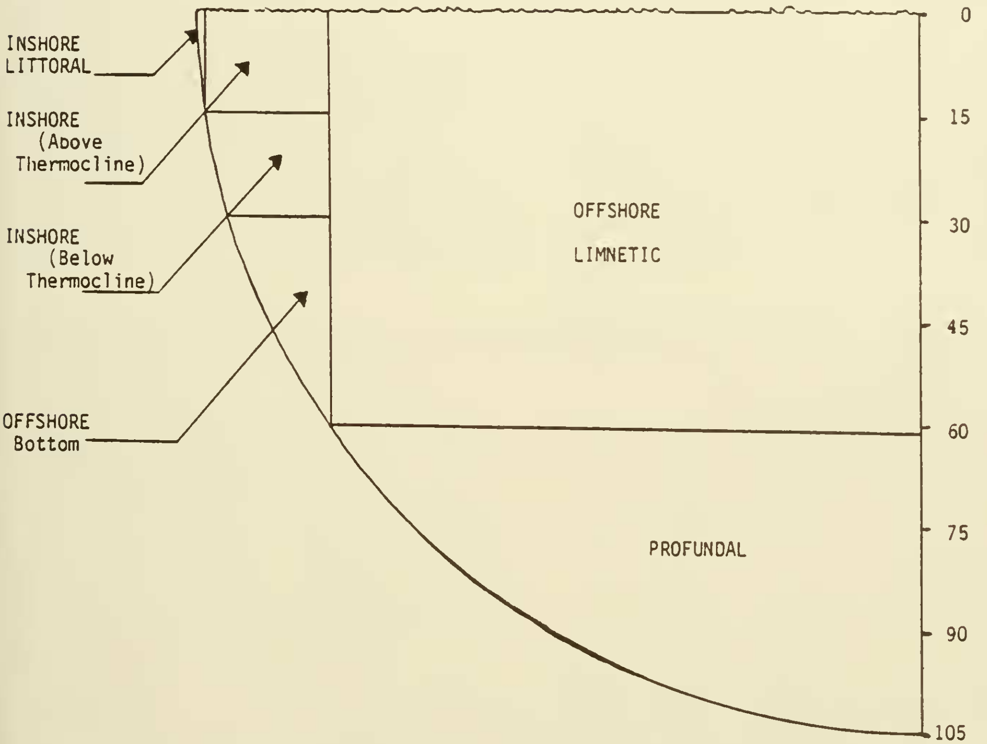
Percent species composition and C/f data from our gill netting program were compared with similar gill net data collected by the Nevada Department of Fish and Game in

TABLE 4. Percent species composition and catch-per-unit effort of fish in six habitat types of Pyramid Lake from June through October 1977, and a numerical relative abundance estimate weighted by the volume of water in each habitat (derived from C/f × volume):

Percent of total lake volume	Habitat	Depth zone	Bottom depth (m)	Number of samples	Catch statistic	Fish species: Cutthroat trout	Cui-ui	Tahoe sucker	Tui chub	Sacramento perch	TOTAL
1.27	Inshore littoral	Bottom	0–15	40	Percent	1.3	1.2	13.9	83.0	0.6	100
					Catch/net	2.8	2.4	29.1	173.0	1.3	208.6
9.30	Inshore below thermocline	Bottom	23	29	Percent	9.1	0.3	21.1	69.5	0.08	100
					Catch/net	7.8	0.3	18.1	59.7	0.07	86.0
10.65	Inshore above thermocline	Surface (0–4 m)	23	29	Percent	0.8	0	0	99.2	0.04	100
					Catch/net	0.7	0	0	88.4	0.03	89.1
8.46	Offshore	Bottom	46	30	Percent	10.8	0	11.0	78.2	0	100
					Catch/net	4.3	0	4.4	31.3	0	40.0
50.92	Offshore limnetic water column	Surface to 46 m	90	18	Percent	0.7	0	0	99.3	0	100
					Catch/net	1.9	0	0	290.4	0	292.3
19.40	Profundal	Bottom	61–100	28	Percent	3.0	0	0.19	96.8	0	100
					Catch/net	0.6	0	0.04	18.4	0	19.0
Numerical relative abundance (percent of: summed catch/net × volume)						1.29	0.03	1.38	97.27	0.01	100

the 1950s (Table 6). Tui chubs and Tahoe suckers dominated the catches during both periods. Current cutthroat trout catches averaged much higher than 1954–1958, probably primarily due to stocking rates. Catches of Sacramento perch and carp were relatively low in both timme periods; however, current catch rates are substantially lower for both species. The most obvious change was the reduction of cui-ui C/f by half, and the decrease in its species composition from 4.4 percent in the 1950s to 1.3 percent presently. Direct comparison of gill net catches from the two time periods was impossible, however, because the nets were not exactly the same. Also, most sampling in the 1950s was designed to capture target species in specific habitats, and the sampling during 1975–1977 was intended to be representative of all species in all lake areas throughout the year.

Two consecutive years (1976 and 1977) of data from our netting program, with identical fishing gear and a consistent temporal and spatial sampling design, provided a valid



ECOTYPE	BOUNDRIES (m) HORIZONTAL	BOUNDRIES (m) VERTICAL	Volume m³ X 10⁶	Volume Percent	Surface Area Hectares	Surface Area Percent
INSHORE LITTORAL	0-15	0-15	323.58	1.27	4,411	10.07
INSHORE (ABOVE THERMOCLINE)	15-61	0-15	2,708.04	10.65	18,131	41.41
INSHORE (BELOW THERMOCLINE)	15-61	15-30	2,365.47	9.30	18,131	-
OFFSHORE BOTTOM	30-61	30-61	2,152.67	8.46	13,436	-
OFFSHORE LIMNETIC	61-100	0-61	12,953.01	50.92	21,247	48.52
PROFUNDAL	61-100	61-100	4,934.48	19.40	21,247	-

Fig. 3. Diagramatic representation and relative proportions of stratified ecotypes of Pyramid Lake sampled during 1975–1977 (calculated for lake elevation 1155.2 m).

TABLE 5. Mean weight and relative biomass of fish in Pyramid Lake, Nevada.

Species	Sample weight (g) Mean	Sample weight (g) Maximum	Sample size (n)	Percent weight of total catch (derived from Table 2: percent of mean weight × total catch)	Relative biomass (derived from Table 4: percent of mean weight × numerical relative abundance)
Cutthroat trout	481	5,450	676	10.68	6.41
Cui-ui	1,504	2,500	360	7.46	0.47
Tahoe sucker	186	1,480	286	13.49	2.65
Tui chub	90	830	322	67.34	90.42
Sacramento perch	485	1,200	104	1.03	0.05

documentation of current short-term trends. There was no statistically significant difference ($P > .05$) between 1976 and 1977 in the mean standardized (18-hour) gill net catch for any species (Table 7). The mean catch of Tahoe sucker and tui chub was almost identical during the two years, thus indicating stable populations. The mean catch of Sacramento perch was likewise close for the two years.

For cutthroat trout and cui-ui, the probability of a significant difference in annual means was about 80 percent. Although this probability level is not commonly considered statistically significant, I believe the changes in mean annual C/f for these species may reflect actual changes in fish abundance. The mean C/f of cutthroat was slightly higher in 1977 (3.4 versus 3.2 fish/net). This increase has probably resulted from progressively

TABLE 6. Catch data from 133 overnight gill net sets in Pyramid Lake during 1954–1958 (after Johnson 1958) compared to catch data from 373 overnight gill net sets in Pyramid Lake from November 1975 through December 1977.

Year	Number of net sets	Catch statistic	Kokanee	Trout*	Cui-ui	Tahoe sucker	Tui chub	Carp	Sacramento perch	Lahontan redside	Total
1954–1955	45	Number	27	28	97	512	1,830	3	16	–	2,501
		Fish/net	0.60	0.62	2.16	11.38	40.67	0.07	0.36	–	55.58
		Percent	1.0	1.1	3.8	20.4	73.0	0.1	0.6	–	100
1955–1956	40	Number	48	29	104	498	1,968	3	45	–	2,695
		Fish/net	1.20	0.73	2.60	12.45	49.20	0.08	1.13	–	67.38
		Percent	1.7	1.1	3.8	18.4	73.0	0.1	1.6	–	100
1956–1957	21	Number	0	17	45	154	697	2	14	–	1,027
		Fish/net	0	0.81	2.14	7.33	33.19	0.10	0.67	–	48.91
		Percent	0	1.6	4.3	14.9	67.8	0.1	1.3	–	100
1957–1958	27	Number	2	7	61	247	1,033	3	6	–	1,359
		Fish/net	0.07	0.26	2.26	9.15	38.26	0.11	0.22	–	50.33
		Percent	0.1	0.5	4.4	18.1	76.0	0.2	0.4	–	100
1954–1958	133	Number	77	81	307	1,411	5,528	11	81	–	7,582
		Fish/net	0.58	0.61	2.31	10.61	41.56	0.08	0.61	–	57..01
		Percent	1.0	1.0	4.4	18.6	73.4	0.1	1.0	–	100
1976	177	Number	0	564	225	2,295	11,044	2	47	–	14,177
		Fish/net	0	3.19	1.27	12.97	62.40	0.007	0.27	–	80.10
		Percent	0	3.98	1.59	16.19	77.90	0.014	0.33	–	100
1977	172	Number	0	661	184	2,698	12,766	3	60	123	16,495
		Fish/net	0	3.84	1.07	15.69	74.22	0.017	0.35	0.69	95.90
		Percent	0	4.01	1.12	16.36	77.39	0.018	0.36	0.75	100
Nov. 1975–Dec. 1977	373	Number	0	1,325	415	5,205	23,345	5	108	123	35,526
		Fish/net	0	3.55	1.11	13.95	67.95	0.013	0.29	0.33	87.20
		Percent	0	4.07	1.28	16.00	77.92	0.015	0.33	0.038	100

*During 1954–1958, the "trout" category consists primarily of rainbow trout with a few cutthroat and brown trout.
During 1975–1976, the "trout" category consists primarily of Lahontan cutthroat trout with a few cutthroat-rainbow hybrids.

TABLE 7. One-way analysis of variance to detect a significant difference between 1976 and 1977 mean standardized gill net catches of five fish species from Pyramid Lake. Data were transformed with $\log_{10}(y + 1)$.

Species	Mean catch (number/net) 1976 (n = 177)	1977 (n = 172)	F Statistic	Significance (P)
Cutthroat trout	3.20	3.40	2.02	0.156 ns
Cui-ui	1.29	0.95	1.58	0.210 ns
Tahoe sucker	13.98	13.98	0.45	0.504 ns
Tui chub	66.57	66.46	0.01	0.920 ns
Sacramento perch	0.29	0.33	0.09	0.766 ns

increasing stocking rates of hatchery fish during recent years. Of all species, only the cui-ui exhibited a decrease in C/f for the two-year period (from 1.29 to 0.95 fish/net). Although the within-year catches of this species are quite variable, the reduction in C/f may indicate that the lake's population decreased slightly from 1976 to 1977.

Summary and Conclusions

The fish population of Pyramid Lake is presently composed of the following species (in order of relative abundance): tui chub, Tahoe sucker, Lahontan cutthroat trout, cui-ui, Sacramento perch, Lahontan redside, carp, speckled dace, largemouth bass, and mosquitofish. The first five species comprise over 99.9 percent of the population; the others are of almost negligible importance to the ecosystem.

Tui chubs and Tahoe suckers, taken together, account for over 99 percent of the total fish population of Pyramid Lake by numbers and about 93 percent by weight. These cyprinids provide the primary forage base for the most important game fish in the lake—the Lahontan cutthroat trout.

Populations of tui chub, Tahoe sucker, and Sacramento perch are currently stable in Pyramid Lake. The Lahontan cutthroat trout may be increasing in abundance, probably due to hatchery stocking rates. The adult cui-ui population may be decreasing in abundance during 1976–1977, probably due to attrition of the older age classes, limited hatchery reproduction, and negligible natural reproduction.

Time, space, and fishing gear selectivity introduce variation that must be accounted for in relative fish abundance estimates. A sampling design stratified by the most important habitat types provides catch/effort data that can be weighted by the proportion of the total volume of the lake that each habitat represents; this approach provides the most reliable estimate of numerical relative fish abundance in lakes. It is important to consider the species specific size composition and relative biomass of the fish population, especially in terms of the bioenergetics of the ecosystem.

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